

Rootstock Breeding for Stone Fruits

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Abstract

Over the last 20 years stone fruit rootstock development has begun shifting from seedling to clonal types, many of interspecific origin. Publicly funded breeding programs have produced most of these rootstocks due to the time, cost, and risk associated with their development; however, private industry is emerging as a significant contributor of many of the newer rootstocks. Particularly noteworthy among recent releases has been the incorporation of resistance to soilborne diseases, nematodes, waterlogging and vigor control, the last most notably in recent cherry rootstocks. Nevertheless, despite the remarkable progress in the development of clonal stocks, seedling rootstocks still dominate most stone fruit industries around the world, if only because of their relatively low cost, ease of propagation, and proven utility. Many opportunities and challenges remain to be addressed in the areas of disease and insect resistance, adaptation to biotic and abiotic stresses, graft compatibility, and rootstock influence on scion performance and fruit quality. Biotechnology is beginning to show potential in accelerating rootstock development. With the development of markers to assist selection for difficult to evaluate traits, new rootstocks with resistance to multiple diseases are feasible. Future prospects for breeding are presented.

INTRODUCTION

Several surveys have been undertaken to determine the relative importance of the various “problems” facing stone fruit industries around the world. The peach (*Prunus persica*) industry has received the most attention, if only because of its large size, hence economic importance, relative to other stone fruit crop industries. Results of two of these surveys are summarized in Table 1. Relative order of importance changed little between 1982 and 1997. At this time it would appear that the need for waterlogging tolerance has been alleviated somewhat by recent releases. This factor was the only one that moved down significantly in importance since the earlier survey. Given the number of rootstock releases that offer some relative promise for most of the problem areas listed, this might seem surprising at first. However, given that orchard life expectations for stone fruits range from 15 to 25 years or longer, adoption is an inherently slow process. This may also be due in part to the fact that many interspecific rootstocks change other “non-target” characteristics of the finished tree, for example, vigor or bloom date which require changes in management that growers may not wish to change. Additionally, many “problem” sites have more than one limitation and require that a new rootstock incorporate resistance to multiple problems for successful adaptation. In many cases, new rootstocks are probably best suited for regional or prescription/niche planting rather than broad use over a large industry. Regional testing is the only way to determine each rootstock’s best adaptation.

Priorities vary from one stone fruit crop to another. Rom (1991) has summarized priorities for apricots (*P. armeniaca*) which generally agreed with those cited for peach. Nematodes were of less importance and one particularly vexing issue with apricot was that of scion/rootstock graft compatibility. However, Rom noted that priorities also varied

widely between growing regions. Ramming and Cociu (1991) noted that priorities for plum (*P. domestica*, *P. salicina*) rootstocks were generally similar to those for peach. Perry (1987) noted priorities for cherry varied considerably depending on scion type. For sweet cherry (*P. avium*), the first and foremost need in rootstocks was for size reduction followed by increased scion precocity and compatibility. For sour cherry (*P. cerasus*), size control was a low priority due to its much lower inherent vigor (compared to sweet cherry). Fortunately, many stone fruit species can be budded onto other *Prunus* species. As a result peaches, plums, apricots and almonds (*P. amygdalus*) often can be budded onto rootstocks developed for each other. In this way, progress made in developing waterlogging tolerant rootstocks for plum cultivars, e.g., Ishtara, also can be used advantageously as a rootstock for peaches, apricots or almonds.

Unlike scion cultivar development, for which evaluation of each generation can take as little as 2–3 years to complete, evaluation cycles for rootstock programs, especially those addressing traits affecting longevity, may require 7–10 years to complete. However, improved methodologies and new technologies have provided significant improvements in evaluation efficiency for some problems and crops.

If only because of space constraints, this presentation must be limited in its scope and depth; therefore, the reader is encouraged to consult other resources pertinent to breeding objectives, progress and available germplasm for stone fruit rootstock development, including Cummins and Aldwinckle (1983); Janick and Moore (1996a, b); Moore and Ballington (1991); and Rom and Carlson (1987).

PROGRESS

Nematodes

One of the most intensely active areas of stone fruit rootstock breeding has been for nematode resistance. Most production areas around the world have significant problems with one or more species of nematode.

1. Root-knot (*Meloidogyne spp.*). Thanks in part to the importance of this pest in many production areas and also to the relatively straightforward inheritance of resistance, many new rootstocks (mostly for peach or plum) have been developed with resistance to one or more species of *Meloidogyne* and released in the last 10 years. While not all production areas are infested with the same species, several are commonly found worldwide, including *M. incognita*, *M. javanica*, and *M. arenaria*. Other less common species are significant problems in certain locales, such as *M. hapla*, *M. hispanica*, and an incompletely identified *Meloidogyne* species that at present is known only in Florida in the United States (A. Nyczepir, pers. commun.).

Resistance to the most common *Meloidogyne* species has been identified in peach and plum germplasm (Layne, 1987; Esmenjaud et al., 1994; Fernandez et al., 1994; Pinochet et al., 1999) and will not be discussed further here. Resistance to the as yet unidentified *Meloidogyne* species in Florida has also been identified (Sherman et al., 1991; Rubio-Cabetas et al., 2000). Screening methodologies are somewhat laborious, involving either field, tank or greenhouse assays. Recent improvements in methodology offer greater efficiency and reliability (Esmenjaud et al., 1996a; Lu et al., 2000). Progress in the determination of the inheritance of resistance to this pest (Esmenjaud et al., 1996b; Lecouls et al., 1997; Lu et al., 2000; Rubio-Cabetas et al., 2000) and the identification of markers (Lu et al., 1998; Lecouls et al., 1999) represent significant progress. This is one of the more mature areas in stone fruit rootstock development and many programs are making significant progress in developing broadly resistant rootstocks for the industries they serve.

2. Ring (*Mesocriconema xenoplax*). The Ring nematode is a primary factor predisposing peach trees to peach tree short life (PTSL) (Nyczepir et al., 1983; Nyczepir, 1990). Attempts to identify resistant *Prunus* germplasm have met with little success (Westcott et al., 1994; Nyczepir et al., 1996). Interestingly, peach trees on Guardian (BY520-9) rootstock display markedly greater resistance to PTSL than when budded onto Lovell

even though Guardian and Lovell support similar populations of ring nematodes (Nyczepir et al., 1996).

3. Lesion (*Pratylenchus* spp). Two species dominate most research interests, *Pratylenchus vulnus* and *P. penetrans*. Although a recognized problem in many stone fruit production areas worldwide, there is still much work to be done in the development of commercial rootstock materials with significant levels of resistance. Evaluation methodologies for many stone fruits have been developed (Potter et al., 1984; Culver et al., 1989) and some sources of resistance identified (Layne, 1987; see Iezzoni et al., 1991; Ledbetter, 1994; Alcaniz et al., 1996; Melakeberhan et al., 1997; McFadden-Smith et al., 1998; Pinochet et al., 2000). However, only a few commercial materials have been released to date. Screening for resistance is laborious and mode of inheritance is still unknown.

4. Dagger (*Xiphinema* spp). *Xiphinema americanum* and *X. rivesi* are the principal species involved in the transmission of Tomato Ringspot Virus (TmRSV), the causal agent of *Prunus* stem pitting and *Prunus* brown line disease. Little progress has been made in the identification of sources of resistance to these nematodes.

Disease Resistance

Considerable progress has been made in the identification of sources of resistance to various diseases. More importantly, several rootstocks have been released for commercial use.

1. Fungi (*Armillaria*, *Phytophthora* and others). Several species are known to attack stone fruits, chief among these in importance are *Armillaria mellea*, *A. tabescens*, and *A. ostoyae*. Various sources of resistance to *Armillaria* species have been identified (Thomas et al., 1948; Duquesne et al., 1977; Raabe, 1979; Proffer et al., 1988; Guillaumin et al., 1991; Loreti, 1997; Beckman et al., 1998), and some progress has been made in the development of rootstocks with resistance to *Armillaria mellea*. 'Ishtara' and 'Myran', both complex plum × peach hybrids, reportedly are significantly more resistant to *A. mellea* than are peach seedlings (Beckman and Cummins, 1991a and 1991b). Unfortunately, this resistance does not appear to extend to *A. tabescens*, another important species (Beckman and Pusey, 2001). Therefore, regional development may be needed to provide suitable improvements. In general, plum species native to the production region appear to provide the most usable resistance to this organism, and most programs attempting to develop resistant stocks for use with peach, plum, apricot and almond have utilized such germplasm. Currently, resistant stocks for cherry are less promising, with the search for suitable sources of resistance continuing (A. Jones, pers. commun.) to expand upon the marginal resistance of *P. avium* found by Proffer et al. (1988).

Until recently, field screening on *Armillaria*-infected sites was the most utilized technique for evaluation, but the use of infected plant tissues in conjunction with natural inoculum on field sites (Beckman and Pusey, 2001) or under artificial conditions (Proffer et al., 1988) has been shown to accelerate infection and mortality markedly, reducing screening time. Nevertheless, screens typically take years to complete and more progress in evaluation methodology is needed. Ultimately, markers for resistance would be a profound advancement. Considerable groundwork has been laid in the development of *Armillaria*-resistant rootstocks, and new materials should be forthcoming to augment the few materials currently available.

Phytophthora often is involved in tree decline and death on waterlogged sites. Invariably, damage is worse when both factors are present and when the problem occurs during the growing, rather than dormant, season. Several species of *Phytophthora* have been demonstrated to be pathogenic on *Prunus*. Screening methodologies have been developed and some progress made in identifying useful differences in germplasm (Mircetich and Matheron, 1981; Wilcox and Mircetich, 1985; Wicks and Lee, 1985; Cummins et al., 1986; Mircetich and Browne, 1989; Cummins and Beckman, 1991; Beckman and Cummins, 1991a, b; Jacobs and Johnson, 1996; Beckman, 1997; Wertheim, 1998). Screening of *Phytophthora* resistant or tolerant *Prunus mahaleb* rootstocks for

cherries is currently underway at University of California-Davis (T. DeJong, pers. commun.).

Somewhat less progress has been made with other important soilborne diseases including *Fusarium*, *Phymatotrichum*, *Pythium*, *Rhizoctonia*, *Rosellinia*, and *Verticillium*. In some cases, these are significant problems in established industries, while in others they prevent the establishment of an industry in climates otherwise conducive to fruit production.

2. Bacteria and MLO's (Crown Gall, Bacterial Canker, X-disease). Germplasm sources have been identified with resistance to crown gall (*Agrobacterium tumefaciens*) (Smith, 1925; DeCleene and DeLey, 1976; see Iezzoni et al., 1991; Stylianidis et al., 1992; Loreti, 1997). Differences in susceptibility have generally been small in current commercial material (Layne, 1987; Peirronnet and Salesses, 1996). Recent work (Bliss et al., 1999) has identified germplasm with potentially useful levels of resistance that should be helpful in the development of rootstocks for peach, plum, cherry and almond. Given the progress in screening methodology and the identification of useful variability, the prospects for development of crown gall resistant rootstocks appear bright.

Bacterial canker incited by *Pseudomonas syringae* is a significant problem on all stone fruits. In most stone fruits, rootstock selection is a primary management tool for dealing with this problem. Peach tree short life (PTSL) specifically refers to the manifestation of this disease, often in conjunction with winter injury, in the southeastern United States. However, it also afflicts peach trees in California (Bacterial Canker Complex), South Africa, Brazil, and Australia. Similar symptoms have been observed on most, if not all, of the *Prunus* species tested on a PTSL site in the southeastern United States (T. Beckman, unpubl. data). Many of the species afflicted were not commercially utilized materials. Considerable progress has been made in identifying rootstock selections with resistance to PTSL and bacterial canker (see Rom and Carlson, 1987 and ref within; Cummins, 1995; Loreti, 1997). The recently introduced 'Guardian' (BY520-9) has demonstrated significantly greater resistance than existing commercial stocks and is now dominating the southeastern US peach industry where PTSL has been a significant cause of premature tree mortality for several decades (Okie et al., 1994a). PTSL resistance screening still relies primarily on field tests, which can take up to 7 years to complete (Beckman et al., 1993; Okie et al., 1994b; Nyczepir and Okie, 1996). Hence, there is considerable interest in the development of markers to accelerate breeding progress.

Selection of cherry rootstocks with less susceptibility to bacterial canker is of interest worldwide, but has been, as yet, rarely practiced, presumably due to few good choices. While 'F.12/1', 'Colt', and the MxM series have been reported to have somewhat reduced susceptibility, only 'Charger' (*P. avium*) has been noted to be "resistant" (Webster, 1996; ASHS, 1997; Wertheim, 1998). The development of lab screening tests by Krzesinska and Azarenko (1992) and Bedford et al. (2002) should help speed identification of further sources of resistance in cherry.

Cherry rootstock tolerance of Western X disease, caused by a mycoplasma-like organism (MLO), remains an elusive goal. Mahaleb, 'MxM 2' and 'MxM 46' (presumably hybrids of *P. mahaleb* × *P. avium*) are considered to be "resistant" (Uyemoto et al., 1991); however, in a grafted tree, this resistance is manifested at the graft union by blockage of MLO movement (and, unfortunately, necessary plant nutrients) from the scion into the rootstock, causing rapid scion death. The susceptible rootstocks Mazzard, 'Colt' (*P. avium* × *P. pseudocerasus*), all Gisela interspecific rootstocks tested thus far, and 'Damil' (*P. × dawykensis*) exhibit a slow decline following X-disease infection.

3. Viruses (TmRSV, PNRSV, Prune Dwarf). Tomato Ringspot Virus (TmRSV) is a serious problem for *Prunus* species in that it causes Prunus stem pitting and brownline disease. Trees infected with this pathogen decline and ultimately die in most cases. The virus is transmitted by the dagger nematode, and control procedures usually have centered on control of the nematode and the alternate weed hosts for the virus. Resistance to the virus has been demonstrated in plum, i.e. Marianna 2624, but has yet to be identified in

other *Prunus* species. An assay for evaluating plant resistance to the virus has been demonstrated and could be used in a breeding program (Hoy and Mircetich, 1984; Cummins and Gonsalves, 1986; Halbrendt et al., 1994).

Mild strains of two common ilarviruses, prunus necrotic ringspot (PNRSV) and prune dwarf (PDV), commonly infect mature sweet cherries worldwide, with little or no negative impact for cherries grown on Mazzard or Mahaleb rootstocks. However, when these viruses move from the point of pollen-borne infection (young flowering shoots) to the graft union of a hypersensitive or sensitive rootstock, rapid or gradual mortality may result (Lang et al., 1997; Howell and Lang, 2001). This sensitivity appears to be carried strongly by the *P. fruticosa* parent used in many of the crosses from the Giessen rootstock breeding program, as well as more variably by one of the *P. cerasus* ('Leitzkauer' or 'Schattenmorelle') or *P. canescens* parents. However, the strong susceptibility carried by the Giessen *P. fruticosa* is not species-wide, as the MSU cherry rootstock breeding program has several selections with *P. fruticosa* parentage that have tested as tolerant to ilarviruses (A. Iezzoni and W. Howell, pers. commun.).

Insect Resistance

Peach tree borers are one of the most important insect pests attacking fruit tree rootstocks. Recommendations for their control are a standard part of grower management in virtually all stone fruit industries. This area would seem to be of burgeoning importance, given the possibility of future withdrawal of important pesticides needed for control of borers (*Synanthedon* spp. and *Capnodis* spp.) and root weevils (*Pachnaeus* spp.) (Sherman and Mizell, 1995). Reports of resistance to peach tree borer (*Synanthedon* spp.) in peach have yet to be confirmed and utilized (Weaver and Boyce, 1965; Chaplin et al., 1974; Chaplin and Schneider, 1975; Puterka et al., 1993). The identification of resistance to *Capnodis* spp. in almond germplasm (Mulas, 1994) is promising, particularly given the possibility that it appears to be correlated with prunasin content, which may provide a more convenient screening procedure than artificial infestation of candidate rootstock lines.

Although the development of alternative control procedures and resistance breeding will be difficult and require close collaboration with entomologists, it appears to be an almost certain necessity given the likelihood that key pesticides soon may be lost. There are alternatives to conventional breeding approaches. Genetic modification of stone fruit rootstocks with genes encoding the BT (*Bacillus thuringiensis*) toxin for the control of *Lepidopteran* pests is one possible avenue. The incorporation and isolation of this trait in the rootstock would presumably be a less controversial issue than its presence in the scion variety and, thus, the consumable fruit. Moreover, if incorporated into an interspecific hybrid that was both resistant to suckering and infertile, the possibility of accidental transfer of the trait into wild *Prunus* would be minimized.

Edaphic Adaptation

1. Calcareous Soils. Peach \times almond hybrids have been a great success for coping with calcareous soils for peach production. Their use in southern Europe, in particular, represents one of the few stone fruit industries dominated by clonal stocks (principally GF677) rather than seedlings. The susceptibility of GF677 to nematodes and crown gall has left room for recent introductions that address these deficiencies. Plum and peach germplasm has been identified which may offer alternatives to almond germplasm for breeding calcareous soil-adapted rootstocks, both for almonds and other stone fruits (Reeves et al., 1985; Crossa-Raynaud and Audergon, 1987; Byrne et al., 1989; Shi and Byrne, 1995). Differences in calcareous soil adaptation of cherry rootstocks have been reported as well (Callesen, 1998; Perry, 1987; Melakeberhan et al., 1995; Webster, 1996; Melakeberhan et al., 2001). Current field and greenhouse rootstock screening procedures for both calcareous and acidic soil conditions suffice, but could be improved upon.

2. Salt Tolerance. Saline conditions are generally a localized problem, but one which may increase in importance as agricultural water resources shrink due to demands placed

on them by human populations. Screening methodology has been developed and used to identify variability in a limited amount of peach, plum and almond germplasm (El-Motaium et al., 1994; Massai et al., 1998; Ottman and Byrne, 1988; Rieger, 2001).

3. Waterlogging Tolerance. Considerable progress has been made in the development of waterlogging tolerant rootstocks, principally from plum germplasm for use beneath peach, plum, apricot and almond varieties; these will not be covered here. This progress can clearly be seen in the decreased importance of this problem between 1982 and 1997 (Table 1). Progress also has been made in discerning useful variability in newer cherry germplasm (Roth and Gruppe, 1985; Beckman, 1988). Given the progress in the identification and development of germplasm, along with necessary methodologies (Rowe and Catlin, 1971; Mizutani et al., 1982; Stassen and Van Zyl, 1982; Andersen et al., 1984; Hassan et al., 1986; Beckman, 1988; Alvino and Zerbi, 1989; Ranney, 1994), waterlogging tolerance appears to be a mature area that is now an ongoing priority of several programs.

4. Drought Tolerance. Water stress is a problem not only in areas with limited rainfall, which are irrigated but may face water shortages as greater demands are made on water resources, but also in areas of significant annual rainfall that increasingly face highly variable periods of unusual drought due to global climatic changes. Several rootstocks, principally almond, peach \times almond and peach \times *P. davidiana* hybrids, have been reported to tolerate drought better than peach seedlings (Wang, 1985). In cherry, it generally is observed that at least some clonal rootstocks, e.g., Colt, and those with *P. cerasus* parentage (e.g., Tabea Edabriz, Gisela 5, and Gisela 6), appear to exhibit water stress more quickly than the seedling rootstocks Mazzard and Mahaleb presumably due to more shallow, less extensive root systems. Others, such as the MxM series, have extensive root systems (Longstroth and Perry, 1996) and are considered to be drought-tolerant (Wertheim, 1998). Rieger and Duemmel (1992) concluded that, in greenhouse tests, peach scion variety characteristics had more influence on tree tolerance than did the physiological characteristics of the rootstock. Hence, it may be that progress may come more rapidly by breeding for drought avoidance, via mechanisms such as root system architecture, than by attempting to breed for physiological tolerance.

5. Nutrition and Low Fertility. Numerous studies have demonstrated that rootstocks influence foliar nutrient content of stone fruit scion varieties (Couvillon, 1982; Werner and Young, 1987; Hanson and Perry, 1989; Brown, 1989; Rozpara et al., 1990; Ugolik and Holubowicz, 1990; Caruso et al., 1996; Neilsen and Kappel, 1996; Webster, 1996; Boyhan et al., 1998; Callesen, 1998). The impact of these relationships on tree performance and/or fruit quality has yet to be demonstrated clearly. Nevertheless, this suggests that it might be possible to correct nutrient deficiencies/excesses, resulting from low/high soil content or availability (e.g. due to soil pH), by a judicious rootstock selection. Low soil fertility has become or is becoming an issue in many traditional stone fruit growing areas throughout the world, particularly in Europe where peach sites are re-used repeatedly, and/or in organic production systems. Initially, the use of high vigor peach \times almond hybrids, such as GF677, gave vigor sufficient for satisfactory peach production in these situations. However, after a generation or two, even greater vigor is needed. At this time, peach \times *P. davidiana* hybrids appear to be promising alternatives for this problem. In cherry, evaluations of the physiological efficiency of nitrogen uptake and/or use by standard and new hybrid rootstocks are currently underway (Zavalloni and Flore, 2002). For specific (and probably modest) purposes, this objective might be a feasible component of a rootstock development program.

6. Cold Hardiness. Low temperature stress involves two issues: first, the hardiness of the rootstock itself. In extreme northern latitudes with adequate snow pack, this is generally not a problem. However, in locations where winter snowfall is inadequate or comes after the occurrence of extreme low temperatures, rootstock damage can be a threat to tree survival. Layne (1974) has documented significant differences in cold hardiness of peach stocks. The second issue is the influence of the rootstock on the hardiness of the scion. A number of rootstocks have been identified which enhance the cold hardiness of peach,

plum, apricot and cherry varieties (Layne et al., 1977; Layne and Ward, 1978; Layne, 1987; Crossa-Raynaud and Audergon, 1987; Perry, 1987; Iezzoni et al., 1991). Breeding for this character can be complicated by the interaction of secondary factors, such as various bark and wood diseases that enter cold-damaged areas of cherry and other stone fruits in the northern latitudes of the USA and elsewhere. Cold hardiness evaluation methodology is a significant limitation to progress, as reliance on 'test' winters is particularly slow and highly variable. Alternative lab-based methods (e.g. Strauch and Gruppe, 1985) offer greater efficiency, though difficulties of their own (see Palonen and Buszard, 1997, for an overview). Markers would be very helpful in this area.

Horticultural Influence

No rootstock will succeed in the stone fruit industries without promoting superior horticultural performance of the scion. Challenging economic conditions, including increased material, labor, and land costs, market competition and overproduction has increased the importance of production efficiency issues. High, reliable, uniform production of premium quality fruit is essential for economic survival. Again, rootstocks can have significant influence on a variety of these important characteristics.

1. Vigor. Several new stone fruit production systems have been introduced in recent years, including palmette, fusetta, perpendicular-V, spindle, solaxe, Spanish bush, and others (Balmer, 2001; Long, 2001). On high fertility sites with vigorous scion cultivars, some reduction in vigor is highly desirable if only for reduced pruning, thinning and picking costs. As an added benefit, vigor reductions are often accompanied by improved fruit quality, in particular red blush, and increased size and sweetness due to reduced shading. New rootstocks, too numerous to list here, have been introduced with varying levels of dwarfing for peach, plum, apricot, cherry, and almond, some imparting scion vigor that is 50% or less than current industry standards. Many more are in development. Of those materials released for commercial trial, probably none have enjoyed a more enthusiastic reception than the new interspecific hybrid rootstocks for sweet cherries, as typified by the Giessen/Gisela and Gembloux clonal series (Lang, 2000). When used with sweet cherries, formerly the largest and most difficult of the stone fruit species to manage, these new rootstocks offer significant possibilities to tame these former giants, and vastly improve labor efficiencies for pruning, training, and harvesting. In general, the greatest levels of vigor control are with rootstocks having significant *P. cerasus* or *P. fruticosa* parentage (Webster, 1996; Callesen, 1998; Wertheim, 1998).

Dwarfing, however, is not the only industry need for vigor manipulation. At the other end of the spectrum are rootstocks which induce higher vigor in scion varieties on low fertility sites, as noted above under "Nutrition and Low Fertility." Furthermore, stone fruits that are harvested mechanically, such as sour cherries, favor rootstocks that will quickly achieve a size suitable for mechanical harvest, providing precocity and productivity are also enhanced.

2. Bloom Time. The potential for a rootstock to either promote or delay bloom probably deserves more attention than it receives. While these effects typically are subtle for scion cultivars grafted onto rootstocks of the same species, such as peach on peach or sweet cherry on sweet cherry, the use of other rootstock species (e.g., peach on interspecific hybrids or sweet cherry on sour cherry) can produce more significant shifts in bloom time (Young and Olcott-Reid, 1979; Young and Houser, 1980; Beckman et al., 1992; Reighard et al., 2001). Such bloom date alterations can translate into proportional harvest date alterations, and/or can be important for spring frost susceptibility or avoidance (Lang et al., 1997).

3. Spring Shock Syndrome. This is a recently reported phenomenon (Malcolm et al., 1999), the cause of which is still understood incompletely. During atypically cool springs in low-chill areas of Australia when soils are slow to warm, peaches on high-chill rootstocks (e.g. 'Golden Queen') lag well behind those on low-chill rootstocks (e.g. 'Okinawa'). This does not appear to be a simple case of delayed bloom, as foliation and tree development lag profoundly through the entire growing season, resulting in delayed

ripening and significant reductions in total crop and fruit size. This is of particular concern since much of the recent growth in stone fruit production, principally peach, has been in low to moderate chilling climatic zones (Fideghelli et al., 1998), which often have unique combinations of disease and edaphic limitations, i.e., coastal regions having sandier soils, root-knot nematodes, and/or nutritional and soil water-holding limitations. Winter hardiness typically is less of a concern. The Spring Shock Syndrome appears to be uniquely tied to such climates and may require a shift in rootstock development priorities for these areas, which have typically relied on adoption of rootstocks from higher chill industries. Focused breeding efforts to develop rootstocks as well-adapted as scion cultivars may be critical for reliable annual production in such areas.

4. Precocity and Productivity. Perhaps just as important as vigor control, many of these new rootstocks, particularly in cherry, induce profound increases in precocity and productivity, which have challenged researchers and growers to develop appropriate crop load management strategies to prevent excessive cropping, reduced fruit size, and insufficient annual growth (Choi and Andersen, 2001; Lang, 2001; Lang and Ophardt, 2000). However, with certain light-bearing cherry cultivars (e.g. ‘Tieton’, ‘Cavalier’), the ability of some new rootstocks to increase flowering spur formation can be the difference between commercial success and failure (Lang, 2000). These important fruiting characteristics are evaluated routinely in large scale regional trials, such as the NC-140 Regional Trials for peach, plum and cherry in the United States, the Working Group on Rootstocks for peach, plum, apricot, almond and cherry in Italy, and the International Cherry Rootstock Trials in Europe. A better understanding of the physiology of these effects (see Molecular Analysis of Key Rootstock Traits below) should lead to a more efficient selection protocol.

5. Graft Compatibility. Scion/rootstock graft compatibility is a critical issue for orchard performance and longevity. It is perhaps more of a problem in cherry, almond, and especially apricot, than in peach or plum. It has been such a particularly vexing issue in apricot that Duquesne (1969) suggested it might be easier to breed apricot varieties with less specific rootstock needs, than rootstocks having compatibility with a wide selection of apricot varieties.

Rapid industry adoption of new sweet cherry cultivar releases, before widespread rootstock graft compatibilities have been tested, has increased the prevalence of reports (e.g. ‘Lapins’, ‘Chelan’, ‘Tieton’) of graft incompatibility, particularly with ‘Mahaleb’ seedling rootstocks. While these appear to be genetic, it is likely (Lang, 2000) that the ilarvirus sensitivity of some of the interspecific cherry rootstocks (discussed above) may explain several of the reports of “delayed graft incompatibility” in European rootstock trials (Wertheim et al., 1998). As all stone fruit rootstock development tends more toward the creation of interspecific hybrids, these compatibility issues will likely take on greater importance. Field trials and direct examination of excised unions are the mainstay of many programs, but these tedious methodologies need to give way to a better physiological understanding of the mechanisms involved so that more efficient evaluation methodologies can be developed, possibly in conjunction with marker assisted selection (MAS).

Graft compatibility between scion and rootstock materials of the same species is often taken for granted, although in some species (e.g. apricot), this is not necessarily a safe assumption. Surprisingly, in several peach rootstock trials reported from the US and Canada and a cherry trial from Poland, the most efficient performer was the own-rooted scion cultivar (Table 3), which often displayed lower vigor, both desirable characteristics. Whether this is an indication of incompatibility in the traditional sense, or more an expression of mechanical interference due to imperfect joining of tissues, remains to be seen. This might seem more an intellectual curiosity, but as markers are developed for important traits, it may become feasible to incorporate important rootstock traits into scion cultivars for use as own-rooted cuttings. Even with current breeding and screening techniques, it should be possible to incorporate resistance to root-knot nematodes into scion cultivars at this time. Not having to bud or graft finished trees offers both cost and

time savings to offset part of the cost of clonal propagation. Efficient protocols have been developed for peach (Couvillon and Erez, 1980; Coston et al., 1983) and should be feasible for the relatively easy to root plums, though cherries remain quite difficult (W. Proebsting, pers. commun.). Own-rooted trees of 'Stanley' plum have been recommended for avoidance of stem-pitting, which develops in grafted 'Stanley' trees that are infected subsequently with TmRSV (Cummins and Gonsalves, 1986). Own-rooted trees of several peach varieties appeared to be less susceptible to stem-pitting than conventional grafted trees (Byers and Yoder, 1994) and have exhibited higher levels of nutrients (Couvillon, 1982). However, own-rooted trees were shown to be more susceptible to PTSL (Reighard et al., 1990).

6. Fruit Quality. Rootstocks capable of improving the fruit quality attributes of the scion variety would be of great interest. There appear to be some possibilities in this area, though many of the effects reported to date have been relatively subtle, negative, or inconsistent, particularly for fruit size. It is often difficult to separate apparently negative effects on fruit size from the combination of the positive traits of reduced vigor and increased productivity that can lead to imbalanced crop loads if not managed properly (Lang, 2000). Potentially useful rootstock influences on fruit maturity have been described for some stone fruits (Beckman and Cummins, 1991a; Beckman et al., 1992; Moreno et al., 1995). The development of an understanding of the physiological basis of these effects will be important.

Interstems

Some mention of interstems is appropriate here. While obviously incapable of directly affecting below ground issues such as soilborne diseases, insects, waterlogging, low fertility, etc., interstems have been shown to provide hardier trunks (Crossa-Raynaud and Aduergon, 1987; Grzyb and Rozpara, 1994), control vigor (Roberts and Westwood, 1981; Grzyb and Rozpara, 1994; Rozpara et al., 1998), delay bloom and fruit maturation of peach (Reighard, 1998); improve fruit quality, vigor control and yield for sweet cherry (Larsen, 1970; Larsen and Patterson, 1981; Larsen et al., 1987), and influence foliar nutrient content in cherry (Rozpara et al., 1990). However, an unavoidable yet significant limitation to their utilization is the added time and cost associated with their production. Furthermore, issues such as graft incompatibility and virus sensitivity/hypersensitivity remain the same for interstocks as for rootstocks.

FUTURE WORK AND NEEDS

Preservation and Exchange of Germplasm

All breeding programs need germplasm as foundational, raw materials. Many recently introduced rootstocks are interspecific hybrids of conventional rootstock species with "exotic" unimproved species that often have no precedent in rootstock usage. A case in point is the USDA rootstock program in Georgia. Many of this program's *Armillaria*-resistant rootstock selections are hybrids with native North American plum species, which as a rule are woefully under-represented in the US Germplasm Repository system. Much of the "available" diversity in these native species is currently stored solely in the breeding collections of the stone fruit breeding programs outside the relative safety of the repository system. At the turn of the century, several hundred fresh market plum cultivars were available that were either selections or hybrids with native North American species (Wight, 1915). However, these were rapidly displaced by the introduction of improved plum cultivars utilizing introduced *P. salicina* materials. Today, barely a handful of the native species-based materials still exist, yet these and the native species from which they were developed have tremendous potential for utilization in solutions for many of our modern problems (Beckman and Okie, 1994). Moreover, much of the wild diversity has disappeared, either because of intentional eradication efforts to reduce wild reservoirs of diseases and insect pests, or because of land development. This is a worldwide problem and a troubling one.

As regionally-oriented stone fruit production industries grow and begin to provide product to national and international markets, a profound shift in germplasm usage also typically occurs as growers change varieties to suit these larger and often more lucrative markets. Such a shift has been seen in the Mexican peach industries, which utilized seedling land races or local cultivars grafted on locally-adapted seedling rootstocks. More dramatic shifts were seen as Spain's peach industry grew into a major supplier of stone fruit to European Union (EU) markets. Typically, no concerted effort has been made to preserve this potentially valuable germplasm since it is often viewed as "obsolete" and worthless. Nevertheless, some of the most significant advances in rootstock adaptation were made with obscure germplasm, such as hardy peach accessions from northern China that produced clearly superior performers under harsh winter conditions in Canada (Layne, 1987). Germplasm exploration needs our continued support and involvement, but so does the preservation of native and naturalized materials in our own backyards that may be slowly disappearing right out from under our noses.

Efforts have been undertaken to evaluate and describe the variability and possible breeding value of some germplasm, such as the 'Vineyard' peaches in Yugoslavia (Vujanic-Varga et al., 1994; Paunovic and Paunovic, 1996), Spanish peach seedling populations (Badenes et al., 1998), and Mexican peach seedling populations (Perez et al., 1993). With the exception of the 'Vineyard' peaches, only scion characteristics were evaluated. Some material has been collected and is being retained, if only on a regional basis at this time.

We also see an emerging problem as many breeding and development programs move forward in the production of complex interspecific hybrids. These materials often display varying levels of sterility, ranging from reduced flower density and set to complete infertility. In hybrids of both native North American plum species and complex plum hybrids with peach germplasm in the USDA program in Georgia, most interspecific hybrids have been completely infertile, producing non-germinating pollen (if any) and setting no fruit (T.G. Beckman, pers. obser.). This is a problem not only within a breeding program, but also for any external program hoping to build on another's releases. Hence, unlike variety breeding programs, which by definition must release materials capable of being intercrossed, many rootstock programs release materials that functionally are genetic dead-ends. A realization of the consequences of this should engender more, rather than less, cooperation and germplasm sharing between programs. However, the ever-expanding issues of intellectual property rights and their ownership may prove to be an increasingly difficult hurdle. Indeed, many programs already exchange and market material only with severe limitations on the use of that material in breeding programs. It is not unusual for non-propagation agreements to include "reach through" clauses giving the "donor" full rights to any hybrids made in the receiving program, be they F₁ or F₂, clearly a step above the traditional "essentially derived" definition of ownership.

Constraints on the exchange of materials will work against the progress and even survival of small and moderate breeding programs, unless they are part of a "group" of (most likely non-competing) programs that exchange germplasm and ideas freely among themselves. Corporate breeding programs, particularly vertically integrated ones that do not offer their cultivars for sale to the public (leasing them only to licensed growers), will end up becoming more or less 'one-way sinks' for germplasm and technology.

SEEDLING VS. CLONAL TYPES

Despite the clear shift from seedling to clonal types over the last 10–20 years (Table 2), seedling types still rule in most stone fruit industries. Obvious exceptions would be the use of peach × almond hybrids on calcareous soils, i.e., 'GF677' in southern Europe, and the likely large-scale shift to the new interspecific cherry hybrid selections where size control and precocity have been needed so badly. The reasons for the continued dominance of seedling types are obvious: low cost (pennies per plant vs. dollars in some cases) and convenience. The ease with which seedling types can be incorporated into the nursery production scheme should not be overlooked either. In those

industries situated in suitable climates, the comparative ease of direct fall planting of a relatively hard to injure seed is a valuable asset compared to the management-intensive process of transplanting and caring for rooted cuttings or tissue-cultured plantlets. In many industries, the predominant production areas suffer from relatively few limitations and for those problems which seedling types have offered solutions, i.e. root-knot nematodes and PTSL, a clonally propagated alternative may be seen as overpriced. Niche planting is likely to be the most common use for many of the clonal materials produced to date, though this will not be true in some industries. The extensive need for tolerance to calcareous soils and adequate vigor on low fertility sites in many production regions of Europe will continue to drive the use of clonal peach \times almond and peach \times davidiana materials, since no comparable seedling counterpart has been developed.

One significant limitation to the future use of seedling types is the issue of uniformity. Outcrossing in seed production orchards no doubt varies widely but in peach appears to be typically between 2–6% (Hesse, 1975; Beckman, 1998). The impact of these events goes largely unnoticed if only because of our inability to detect such events. The frustrating variability in delayed tree mortality due to graft incompatibility, as with certain seedling cherry and apricot rootstocks, is a clear example of the potential negative ramifications of this genetic variability. Also, as orchard management becomes more intensive in a highly competitive global market, increased uniformity of rootstock performance across various scion varieties will be more important for achieving efficient profitability. Virtually all of the dominant seedling stone fruit rootstocks lack any morphological feature, such as red leaves, to allow visual detection of outcrosses in the nursery setting. If good control of outcrossing, or at least efficient rogueing techniques, could be devised, then even interspecific hybrid seedlings could be made practical. Several potentially useful lines have been proposed and developed (Riggoti, 1942; Bernhard, 1965; Kester and Hansen, 1966; Jones, 1969; Kester et al., 1970; Jones, 1972), but have not enjoyed adoption due, in part, to problems with nursery production efficiency and uncontrolled outcrossing with resulting variability. This area is worthy of more attention.

The use of doubled haploids is another avenue that deserves consideration. In the absence of an outcrossing event, this allows the production of a “seedling clone” of the mother plant (Scorza and Pooler, 1999). Such seedlings could then be handled like any conventionally produced sexual seedling, with the attendant lower production and management costs compared to conventional clones produced via cuttage or tissue culture. A major obstacle is the relative rarity of haploids. Toyama (1974) estimated their rate of occurrence at about 1:1250.

MOLECULAR ANALYSIS OF KEY ROOTSTOCK TRAITS

This is a promising research area, with molecular analyses becoming more routine, automated (such as DNA microarrays), and genetically powerful (with tools such as the *Arabidopsis* genomic library). While such work pertinent to stone fruit rootstock breeding is increasing, little has yet to be found in the scientific literature. In cherry, DNA microarrays have been created to examine rootstock and rootstock-induced scion gene expression, with particular emphasis on genes associated with dwarfing and perhaps graft incompatibility (K-H. Han and G. Lang, pers. commun.). Similarly, a homolog to the *Arabidopsis* flowering-associated gene, *LFY*, has been identified in sweet cherry, and is being used to probe rootstock induction of scion precocity and flower spur formation (G. Lang, pers. commun.). The molecular analysis of such traits is expected to lead to more efficient capabilities for developing and/or evaluating the improved expression of key horticultural or pathological traits in stone fruit rootstocks and grafted scions.

Rootstock Evaluation Methodology

Current testing programs such as the NC-140 in the United States (Perry et al., 2000), the Working Group on Rootstocks in Italy (Loreti, 1997) and the International Cherry Rootstock Trials in Europe (Kemp and Wertheim, 1996), among others, are

laudable in both their aims and progress to date, and will likely continue to grow in their sophistication and usefulness. Most new rootstocks were developed at least in part with some improved resistance to a disease, pest or edaphic limitation. With the possible exception of climatic adaptation, these characteristics are difficult to evaluate accurately in the current regional and international testing trials. Indeed, it would not be practical to evaluate characteristics pertinent to longevity in conjunction with a horticultural trial typically utilizing as few as 8–10 single tree replications, as is the case of the NC-140 trials. Even minimal tree losses during the course of the trial would seriously compromise the collection of meaningful horticultural data. Nevertheless, in the absence of an organized effort to provide meaningful, broad evaluation of the non-horticultural characteristics of these new materials, they will likely be introduced into distant marketplaces with only tentative recommendations for their use in dealing with the very diseases and problems they were developed to address. We propose that some effort needs to be made to provide uniform testing of disease, pest and edaphic performance under realistic field conditions as a counterpart to the horticultural trials currently performed. Necessarily, these will have to be limited in number, as probably only regional trials will be practical and affordable, especially given the larger replication needed to evaluate problems that can result in the death of non-resistant materials.

For the evaluation of rootstock impact on fruit quality issues, an economic analysis would be a useful addition to typical horticultural testing. In many markets, there is currently no economic incentive to provide improved quality characteristics beyond some minimal base level, for example % soluble solids. However, in virtually all markets there is a premium paid for larger size fruit, in which case some trade-offs (e.g., reduced total yield) can be more than made up with the premium paid for larger fruit. Appropriate application of pricing structures at each trial location would help growers and extension personnel sort out which rootstock may maximize economic return. Additionally, the type of long-term production data typically generated in large scale performance trials lends itself to a variety of statistical analyses to reveal genotype \times environmental interactions and performance stability (Olien et al., 1991), as well as relative production risk (Harper and Greene, 1998). Such analyses would provide valuable feedback to breeding programs and better inform growers and extension personnel.

IMPACT OF MARKER ASSISTED SELECTION (MAS)

Although MAS holds promise for all areas of rootstock breeding through reduced cost and increased efficiency (and speed) of evaluations, it has the best potential for profound impact on those characteristics that are particularly difficult to evaluate. This is because the testing procedure itself relies on a currently expensive methodology, and/or the opportunity to score populations is infrequent. Either problem can severely slow progress. Field evaluation of cold hardiness or dwarfing are examples. Diseases that cause tree mortality well after establishment would also be prime candidates for the development of markers. Field evaluation for resistance to both PTSL and *Armillaria* root rot is difficult not only because of the lack of uniformly infected field sites, but also because field screens typically require at least 5–7 years to achieve sufficient mortality to allow differentiation of the resistant lines from the susceptible. Efforts are underway to develop markers for many important traits, including graft compatibility, precocity, and resistance to root-knot nematodes, PTSL and *Armillaria* root rot.

Those traits controlled by only a few genes are more likely to provide usable markers than are those controlled by many genes. The investment in effort to produce and accurately score a suitable segregating population to generate the initial marker trait associations, will doubtlessly require substantial effort in many cases. Molecular markers having few alleles per locus such as RAPDs and AFLPs are likely to have low transferability rates between pedigrees and may require mapping in each segregating population. Microsatellite (SSR) based markers which are typically codominant and have multiple alleles per locus are likely to be much more informative in inbred species such as peach.

Another application of this technology is the use of markers for the purpose of identifying rootstock cultivars (Cantini et al., 2001). This has utility not only for the protection of intellectual property rights, but also for the field verification of rootstock identity (Struss et al., 2002), which is often difficult (if not impossible) in nursery or orchard situations, yet would be extremely helpful when diagnosing performance problems.

CONCLUSIONS

Considerable progress has been made in recent years in the development of better-adapted rootstocks for stone fruits. Indeed, in a few cases, such as waterlogging tolerance for peach, progress has been such that there has been a significant reduction in the perceived importance of the problem. Progress has been made in the development of more efficient screening procedures, which in turn leads to the identification of useful variability, both of which by necessity precede the development of commercially useful materials. Modern genetic engineering technology is starting to realize much of its promise in the identification of markers that will reduce reliance on tedious, expensive, long-term field trials and thus accelerate progress. Much good scientific work and challenges remain.

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Tables

Table 1. Ranking of peach rootstock problems internationally: 1982¹ vs. 1997².

Problem	1982	1997
Nematodes	1	1
Waterlogging	2	6
Soil diseases	3	3
Calcareous soils	4	2
Vigor control	5	4
Climate adaptability	6	5

¹After Rom, 1984

²After Fideghelli et al., 1998.

Table 2. Rootstock introductions (US) for temperate fruit crops (through 2001). Source: ASHS, 1997; Okie, 1997, 1999, 2002.

Fruit	Thru 1970		1971–1990		1991–2001		Total	
	Sdlg.	Clonal	Sdlg.	Clonal	Sdlg.	Clonal	Sdlg.	Clonal
Almond	0	1	1	2	0	2	1	5
Apricot	0	1	1	0	0	2	1	3
Peach	12	0	0	0	9	17	21	17
Plum	0	3	0	6	0	2	0	11
Cherry	3	1	0	6	0	13	3	20
Apple	3	40	0	10	0	3	3	53
Pear	0	0	0	17	0	1	0	18

Table 3. Yield efficiency of own-rooted peach and cherry trees compared to conventional grafted trees.

Trial	Reference	Scion cultivar	Cum. yield efficiency (kg/cm ²) ¹	% of trial mean ²	Rank/total ³
Clemson, SC	Reighard et al., 1997	Redglobe	0.97	126	2/20
1984 NC-140, All	Perry et al., 2000.	Redhaven	1.07	109	3/9
1984 NC-140, GA	"	Redhaven	1.81	128	1/8
1984 NC-140, CA	"	"	2.12	116	1/9
1984 NC-140, MI	"	"	1.3	100	7/9
1984 NC-140, NJ	"	"	1.18	113	3/9
1984 NC-140, PA	"	"	1.31	116	1/9
1984 NC-140, AR	"	"	1.21	96	5/9
Rutgers, NJ	Frecon, 1987	Loring	0.29	117	1/2
"	"	Blake	0.15	68	2/2
Warsaw, Poland	Jadcuk, 1998	Schatten-morelle	-	125	1/4

¹ Own-rooted scion

² Expressed as percent of overall trial mean

³ Rank of own-rooted scion/total number of treatments